

Hyoid structure, laryngeal anatomy, and vocalization in felids (Mammalia: Carnivora: Felidae)

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Abstract

Two types of hyoid structure are found in the Felidae. In five species it contains a cartilaginous ligament, in all other species it is completely ossified. Traditionally, it has been hypothesized that the presence or absence of roaring and purring in the acoustic repertoires of Felidae is correlated with these differences in the structure of the hyoid. This character complex has been used as a major criterion in the systematics of the Felidae. The present study brings together all currently available data to test this hypothesis, and discusses new findings on laryngeal anatomy with respect to vocalization and the hyoidean apparatus in the family Felidae.

In the Felidae an incompletely ossified hyoid does not automatically cause a species' ability to roar as this vocalization is restricted to only three of the five species with this hyoid type. All felid species which have been proven to purr have a completely ossified hyoid, but definitive evidence of this vocalization is still lacking in many species with this type of hyoid. Therefore, it is not possible at present to decide whether a fully ossified hyoid automatically causes a species' ability to purr. A further type of vocalization is restricted to those four felid species with a vocal fold morphology differing from that of all other species of the family.

Introduction

RICHARD OWEN (1834) was the first to hypothesize a correlation between hyoid structure (see Figs. 1–3) and the occurrence of the specific type of vocalization called roaring in certain species of the Felidae. Based on the differences he found in the structure of the hyoid between the lion (*Panthera leo*) (felid taxonomy used in this publication follows HONACKI et al. [1982], unless otherwise stated) on the one hand, and other species investigated (cheetah-*Acinonyx jubatus*, caracal-*Lynx caracal*, flat-headed cat-*Felis planiceps*, and domestic cat-*F. silvestris* f. *catus*) on the other, he pointed out (p. 129) that for the lion:

“The larynx is consequently situated at a considerable distance from the posterior margin of the bony palate; but the soft palate is prolonged backwards to opposite the aperture of the glottis, and the tongue is proportionately increased in length. Thus a gradually expanding passage leads from the glottis, where the air is rendered sonorous, to the mouth, and it is not unlikely that the strong transverse ridges upon the bony palate may contribute, with the preceding trumpet-like structure, to give that intonation which is so aptly denominated ‘the roar of the lion’.”

Then, in discussing his findings on hyoid structure in the other felids studied, he stated, “From the difference in the voice, the feline animals might have been expected, à priori, to present some differences in that part of their anatomy which relates to it.”

Pocock's (1916) comprehensive survey of the hyoidean apparatus in the Felidae was based on dissections of 23 species, extending the number of species studied to 24 of the 37 recent Felidae. Pocock confirmed OWEN's morphological findings and also adopted his interpretation of the correlation between hyoid structure and the occurrence of roaring in

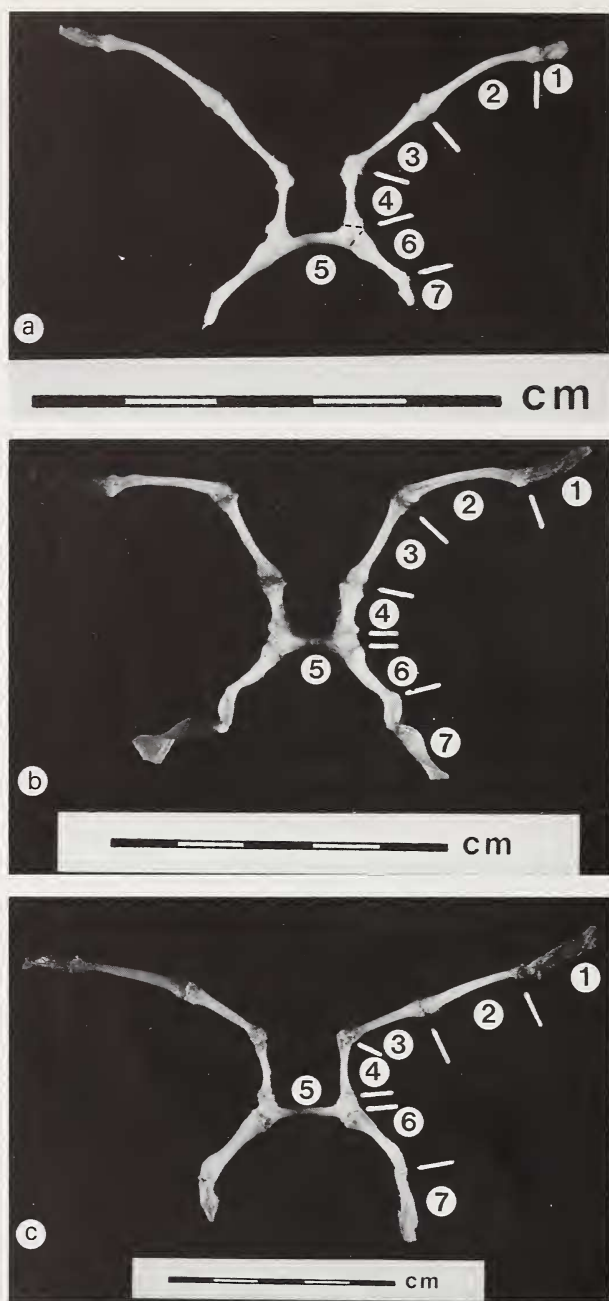


Fig. 1. The hyoid apparatus consists of a paired chain of bony/cartilaginous elements, connected by a single median element, the body of the hyoid. Both chains consist of a cranial and a caudal cornu each. Dorsal view of fully ossified hyoid apparatus of felid species a: domestic cat hybrid (*Felis s. silvestris* × *F. s. f. catus*) ad. ♀ (ZFMK 85.50), b: jungle cat (*Felis chaus*) ad. (ZFMK 86.123), and c: cheetah (*Acinonyx jubatus*) ad. ♀ (ZFMK 86.119). Scale 5 cm. Labeled structures (unilaterally only): 1 = tympanohyoid (cartilage); bones: 2 = stylohyoid; 3 = epihyoid; 4 = ceratohyoid; 5 = basihyoid; 6 = thyrohyoid; 7 = chondrohyoid (cartilage). 1–4 = cranial cornu, 5 = body, 6 and 7 = caudal cornu of hyoid. (In a the border between body and the two cornua is marked on the bones for better visibility)

felids. According to POCOCK, those species producing a roar are lion, leopard (*Panthera pardus*), jaguar (*P. onca*), and tiger (*P. tigris*); and in these the hyoid apparatus is not completely ossified (cf. Fig. 3). The snow leopard (*P. uncia*) is the only other felid species sharing this anatomical character, but its voice was not known to POCOCK. All remaining species of this family very likely have a fully ossified hyoid (cf. Figs. 1, 2).

POCOCK originally stated that the tympanohyal "... generally, if not always, remains cartilaginous through life up to its point of attachment with the bulla." (POCOCK 1916: 222). However, recent textbooks on domestic cat anatomy like CROUCH (1969) or FIELD and TAYLOR (1969) consider it to be a bone, or to consist of tight connective tissue (NICKEL

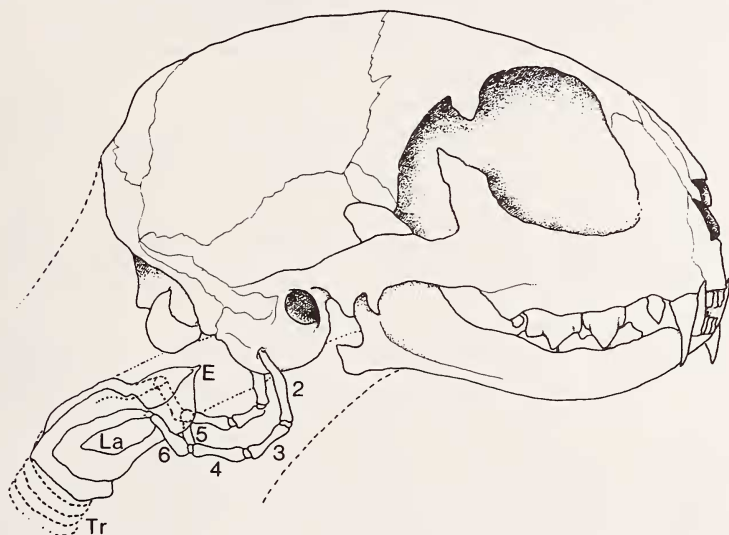


Fig. 2. Attachment of hyoid apparatus to skull and larynx in a felid species with a fully ossified hyoid (schematic drawing by ANNE DAHM). E = epiglottis; La = larynx; Tr = trachea; labeling of hyoid bones as in Fig. 1

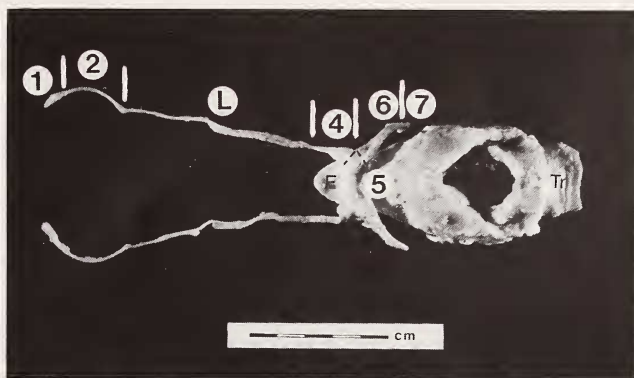


Fig. 3. Hyoid apparatus (still attached to the larynx) of a leopard (*Panthera pardus*) ad. ♀ (ZFMK 89.478), a species in which the hyoid is not fully ossified. The epihyoid is replaced by an elastic ligament (L). Other labeled structures as in Figs. 1 and 2; the tympanohyoid is cartilaginous; scale 5 cm. (Border between body of hyoid and its caudal and cranial cornu is marked on the bones for better visibility)

et al. 1977). The four hyoid specimens in Figs. 1 and 3 clearly show that in these felids the tympanohyal is not bony. In the present paper the statement of a fully ossified hyoid pertains to the hyoid elements 2 to 6 as shown in figures 1 and 2.

To extend and consolidate the hypothesis of a correlation between hyoid structure and vocalization in the Felidae, POCOCK (1916: 229) stated: "Apart from the roar there is another very distinctive feature about the voice of the cats with a normal (i.e. fully ossified [G. P. and M. H. H.]) hyoid. This is the familiar 'purr'. Lions, tigers, leopards and jaguars never purr; on the other hand, such widely different species as cheetahs, pumas, caracals, jaguarondis, and others . . . express . . . that sound. These are interesting differences correlated with the differences in the hyoid apparatus described above . . . The species in which the hyoid is provided with this ligament (instead of the bony epihyale [G. P. and M. H. H.]) roar, but do not purr. All the other species of Felidae with normally constructed hyoid purr, but never roar."

In his later study on the classification of the existing Felidae, POCOCK (1917b) considered these differences so important that they are the major criteria which separate two subfamilies of the Felidae, the Felinae and Pantherinae. The cheetah, as the sole species of the third subfamily, Acinonychinae, is thought to be more closely related to the Felidae, because it resembles them in the structure of its hyoid (cf. Fig. 1c with 1a and b).

Many later studies presenting a classification of the Felidae or dealing in detail with felid systematics largely followed POCOCK's (1917b) concept based on the division of "roaring" and "purring" cats (e.g. NEFF 1982). Even very recent biochemical studies in this field (e.g. WAYNE et al. 1989) include these criteria in their discussion. In a list of the classification of the recent Carnivora, WOZENCRAFT (1989) retained the Felidae and Pantherinae as subfamilies of the Felidae but with a content quite different from POCOCK (1917b), e. g., the Pantherinae also including the lynxes (genus *Lynx*) and the caracal, the marbled cat (*Felis marmorata*) and clouded leopard (*Neofelis nebulosa*). WOZENCRAFT (1989) did not go into detail on the decisive criteria for his system of classification but in the main he followed COLLIER and O'BRIEN (1985), O'BRIEN et al. (1987) and WAYNE et al. (1989) who based their classifications on karyological, albumin immunological distance and isozyme genetic distance data. Yet the reference cited (WERDELIN 1983) for the inclusion of the marbled cat in the Pantherinae does not present any data to support this hypothesis.

In his major study of felid skull morphology, HALTENORTH (1937: 235) expressly questioned the significance of hyoid structure in felid systematics and considered roaring as a plesiomorphic vocalization character in species of this carnivore family. In a very recent study of felid skull morphology SALLES (1992) included hyoid structure as a character and considered a fully ossified hyoid as the plesiomorphic state, but did not recognize subfamilies within the Felidae.

The current study tries to bring together all available data to test OWEN's (1834) and POCOCK's (1916, 1917b) original hypothesis that there is a correlation between hyoid structure and the presence of certain vocalizations in species of Felidae. Furthermore, this study discusses the findings of HAST (1986, 1989) on laryngeal anatomy with respect to vocalization and hyoid structure in felid species. In doing so, it will also provide a basis for evaluating the validity of using these character sets as criteria in felid systematics.

Material and methods

This study, being largely a review, is based on data published in the main papers cited on hyoid structure (OWEN 1834; POCOCK 1916), laryngeal anatomy (HAST 1986, 1989) and vocalization (PETERS 1978, 1980, 1981, 1983, 1984, 1987) in the Felidae. In addition, supplemental data on hyoid structure, laryngeal anatomy and vocalization are also included. Table 1 lists the felid species for which respective data are available.

Data on hyoid structure and vocalization are present for all species listed; laryngeal anatomy is

known in a smaller number. Although the sample size for hyoid structure and laryngeal anatomy in some species is limited to only one specimen, it seems fairly safe to assume that the sample is representative of each species and, more certainly, the family Felidae altogether with respect to these character complexes. The amount of data on vocalization in the individual species is different. There is no species for which a comprehensive structural and functional analysis of its complete acoustic signal system exists. Therefore, statements on vocalization are made with reservations, especially for those species for which only limited data are available (see Tab. 1). Nevertheless, the data on vocalization for the family Felidae, as a whole, are considered sufficient for a comparative survey.

Table 1. Data base on hyoid structure, laryngeal anatomy, and vocalization in the Felidae

Species	Hyoid structure	Laryngeal anatomy	Vocalization
<i>Acinonyx jubatus</i>	+	+	+
<i>Felis aurata</i>	+	—	+
<i>F. bengalensis</i>	+	—	+
<i>F. chaus</i>	+	—	(+)
<i>F. colocolo</i>	+	+	(+)
<i>F. concolor</i>	+	+	+
<i>F. geoffroyi</i>	+	+	(+)
<i>F. manul</i>	+	+	(+)
<i>F. margarita</i>	—	—	(+)
<i>F. marmorata</i>	+	+	(+)
<i>F. nigripes</i>	+	+	+
<i>F. pardalis</i>	+	—	(+)
<i>F. planiceps</i>	+	+	(+)
<i>F. rubiginosa</i>	—	—	(+)
<i>F. serval</i>	+	+	+
<i>F. silvestris</i>	+	+	+
<i>F. temmincki</i>	—	—	(+)
<i>F. tigrina</i>	+	+	(+)
<i>F. viverrina</i>	+	—	(+)
<i>F. wiedii</i>	+	—	(+)
<i>F. yagouaroundi</i>	+	+	+
<i>Lynx caracal</i>	+	—	+
<i>L. lynx</i>	+	—	+
<i>L. rufus</i>	+	+	+
<i>Neofelis nebulosa</i>	+	+	+
<i>Panthera leo</i>	+	+	+
<i>P. onca</i>	+	+	+
<i>P. pardus</i>	+	+	+
<i>P. tigris</i>	+	+	+
<i>P. uncia</i>	+	+	+

+: character complex studied; —: not studied; (+): limited data [a qualification only used in the 'Vocalization' column in species with poorly known vocal repertoire].

Results and discussion

Hyoid structure and vocalization

Since the early investigations of OWEN and POCKOCK did not deal with vocalization in a technical manner, there have been few serious attempts to define "roaring" as a vocalization of lions and other felid species, in appropriate technical terms. Therefore, it can be assumed that the term "roaring" has usually been applied in its "common use" dictionary definition, e.g. MERRIAM-WEBSTER (1986: 1963): "roar: to utter or emit a full loud heavy prolonged sound (the lions roared)" resp. "roar: the sound of roaring: the deep loud cry of some wild beasts (the roar of a lion)", or OXFORD ENGLISH DICTIONARY (1933): "roar: 1. a full, deep, prolonged cry uttered by a lion or other large beast, . . ." Thus, in the

context of a technical description of felid vocalization, this is a circular definition and is equivocal, in that lions can produce different types of sounds which fit this general description. All the more, therefore, using the term "roaring" for vocalizations of other felid species is equivocal. Definitions in some recent publications like "The roar is a distinct, specific vocalization, very loud and resonant, which is produced by the pantherines – the lion, tiger, jaguar, and leopard." (NEFF 1982: 20), obviously have the same weakness as those given above, and give no criteria for an unequivocal identification of the "roar" in any of these species.

Whereas OWEN did not get into detail on roaring, and thus a critical evaluation of his statement in this respect is not possible, POCOCK's (1916) denotation of roaring in different *Panthera* species but the snow leopard is specific enough to identify those vocalizations for which he used this term (i.e. vocalizations unique to the lion, jaguar, leopard, and tiger). Based on structural analyses (PETERS 1978), it has been shown that certain of the relevant single calls of all four species and of the call types composing the structured call sequences in the first three species, which POCOCK lumped under 'roaring', actually represent different types of vocalizations. Some of these vocalizations are not common to all four of these species, while others are common to many more species of the Felidae. Thus, POCOCK's use of the term "roar" was ambiguous and his hypothesis of a correlation between hyoid structure and the presence of roaring in a species' acoustic repertoire needs to be reformulated and re-examined.

LEYHAUSEN (1950) was the first who attempted to deal with felid roaring in a more technical way, but he did not go into much detail on vocalization structure. However, he pointed out differences in the sound of roaring and its articulation between lion and tiger, and the significance of roaring of hybrids between these two species for the elucidation of differences between the equivalent calls of their parental species. RESCHKE (1960, 1966), TEMBROCK (1962), SCHALLER (1972), and HEMMER (1966, 1968) published definitions of roaring in the Felidae, with the former three authors basing their definitions on bioacoustical analyses.

Referring to SCHENKEL (1966), SCHALLER (1972: 105), in describing roaring in lions, stated that "Roaring represents a graded system, ranging from barely perceptible grunts to full roars, . . ." This definition of roaring includes different types of single calls, either produced in a loud structured call sequence, as roaring "proper", or singly or in series of variable composition and temporal structure at low to medium intensity. SCHENKEL's (1966: 617, 618) original text, in discussing different types of roaring, did not differentiate between roaring as a structured call sequence and the single calls composing the sequence and their specific character. However, he clearly stated that he did not regard all call types involved as belonging to the same graded system. In an earlier treatment of vocalization in the tiger, SCHALLER (1967: 258) held that "Moans and roars are lumped into one category because the sounds represent variations in intensity of the same basic vocalization." Therefore, as in the lion, the term "roaring" in the tiger is applied to different types of single calls as well as to call sequences composed of such calls. Using "roar" in this way, SCHALLER very likely held that these vocalizations are fully equivalent in both species; he also listed (SCHALLER 1972: 452) the leopard as being able to roar. In effect, the ambiguous use of the term roaring was continued by SCHENKEL (1966) and SCHALLER (1967, 1972).

RESCHKE (1960, 1966) and TEMBROCK (1962) both used the German term for roaring ("Brüllen"), with qualifications, and pointed out its ambiguity. In defining different call types and the structured call sequences of certain felid species, they presented unequivocal characterizations of most relevant vocalizations in the *Panthera* species and some other felids but did not comment at all on the postulated correlation of the presence of roaring in a species and its hyoid structure.

Though not based on proper bioacoustic analyses, HEMMER (1966) presented a relatively clear definition of roaring in the lion, leopard, jaguar, and tiger. Because he was well

aware of the composite nature of the structured call sequences in the lion, leopard, and jaguar and the absence of an equivalent call sequence in the tiger, he aimed at a definition of roaring that would encompass all four species. Thus, the typical roaring sequence of a lion, as commonly understood (very likely also by OWEN and POCOCK in their relevant publications), was not defined as roaring in its entirety but only its intense initial portion (HEMMER 1966: 60–61). Under this object-defined definition of roaring, HEMMER (1966) held that the lion, leopard, jaguar, and tiger do roar, whereas the snow leopard does not roar. In making such a statement this author neglected the differences between the former four species in respect of temporal and intensity patterning of the relevant call series. HEMMER (1966: 76) concluded that, in felids, there is no direct correlation between hyoid structure and vocalization. He based this conclusion on his observation that the snow leopard is able to purr and unable to roar, despite the fact that its hyoid is not fully ossified; this would predict just the opposite situation for these two vocalizations.

In a detailed technical study of vocalization in all *Panthera* species, the clouded leopard and puma (*Felis concolor*), PETERS (1978) did not apply the equivocal term 'roar' as it had been used for different types of vocalizations in various species. For the lion, in which 'roaring' usually was applied to the loud species-specific structured call sequence (see Figs. 4, 5), PETERS (1978) demonstrated that these sequences comprise at least two different types of calls (Figs. 6, 7), one of which is definitely not found in the tiger. All three (very rarely four) call types, however, which can appear in a roaring sequence of the lion may

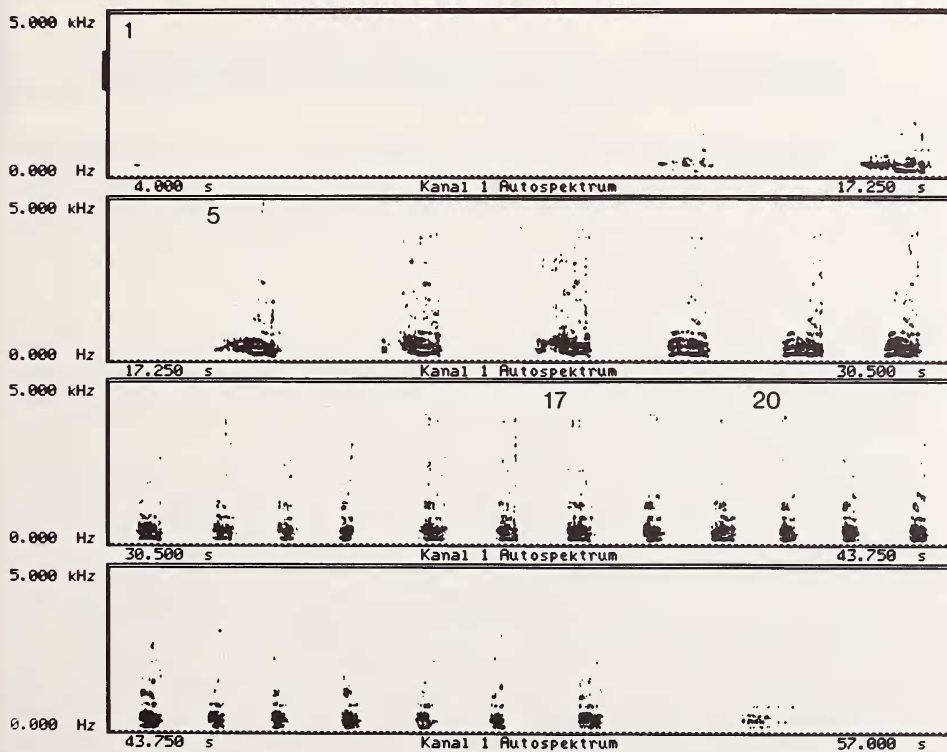


Fig. 4. Continuous sonagram (53 s, partitioned over 4 sonagrams of equal duration) of a complete roaring sequence ('roaring proper') of an adult ♂ lion (*Panthera leo*). Frequency axis (y-axis) represents 5 kHz, time axis (x-axis) 13.25 s in each sonagram. Labeled single calls no. 5 (see Fig. 6) and 17–20 (see Fig. 7) are analyzed once again in more detail

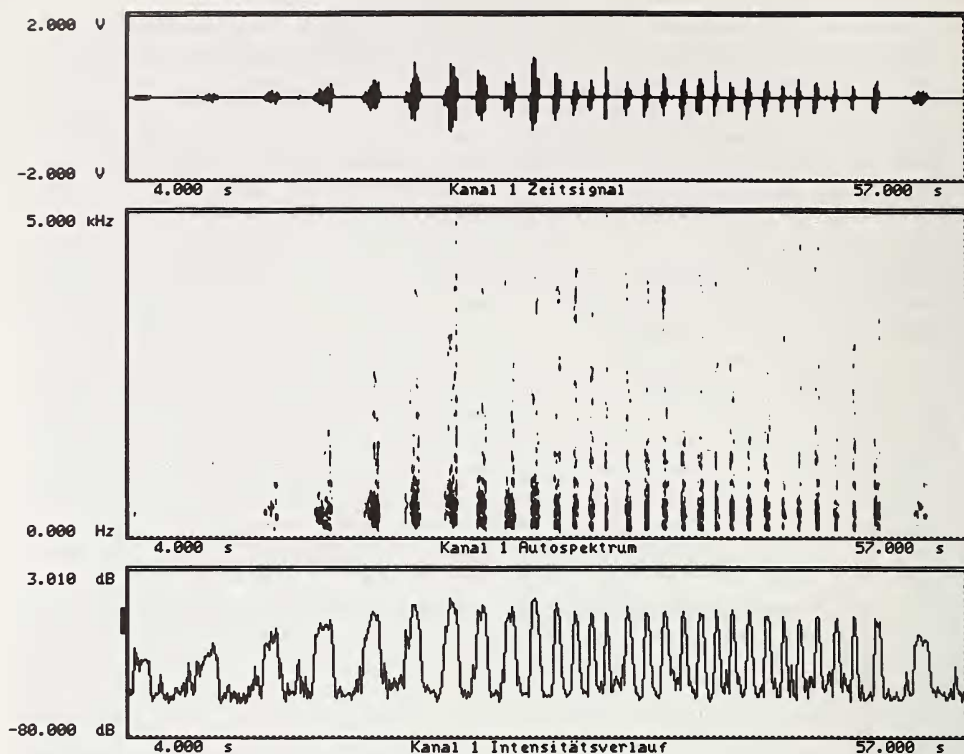


Fig. 5. Oscillogram (top), sonogram (middle) and intensity graph (bottom) of the same roaring sequence as in Fig. 4. X-axis (time) is the same for all (53 s duration), units and their respective calibrations on the y-axes are given. The call types composing the sequence, their succession, the general pattern of their change in intensity, duration and duration of the intervals between them are species-specific for lion roaring

also be present in the equivalent sequence in the structured call series of the leopard and jaguar. The usual form of these series in the latter two species, though, is different from the roaring of lions in that they are equivalent to the second half of the lion roaring sequence.

Like HEMMER (1966), PETERS (1978) concluded that hyoid structure and the occurrence of roaring in the Felidae (defined by reference to the lion's structured call sequence) are not correlated. Thus, with the relevant vocalization of the lion – as very likely understood by OWEN and POCKOCK – as the standard of comparison, the leopard and jaguar have fully equivalent vocalization sequences, whereas the tiger and snow leopard do not. These are the only felid species with an incompletely ossified hyoid. Because of the established differences in the relevant call types and call sequences (under the various definitions of roaring), and as none of these is shared by all five species, and at the same time is not present in any other felid, an incompletely ossified hyoid in a felid species is not necessarily associated with the presence of roaring in this species' acoustic repertoire. Hence the hypothesized direct correlation of roaring and hyoid structure (i.e. an incompletely ossified hyoid) can be refuted. For the first time, this statement was based on technical analyses and definitions of all relevant sound types and call sequences (PETERS 1978).

Similar ambiguity and confusion exist for the definition of purring, the 'counterpart' of roaring within the felid acoustic repertoire, as postulated by POCKOCK (1916). The MERRIAM-WEBSTER (1986) dictionary definition of purr as "a low vibratory murmur of a

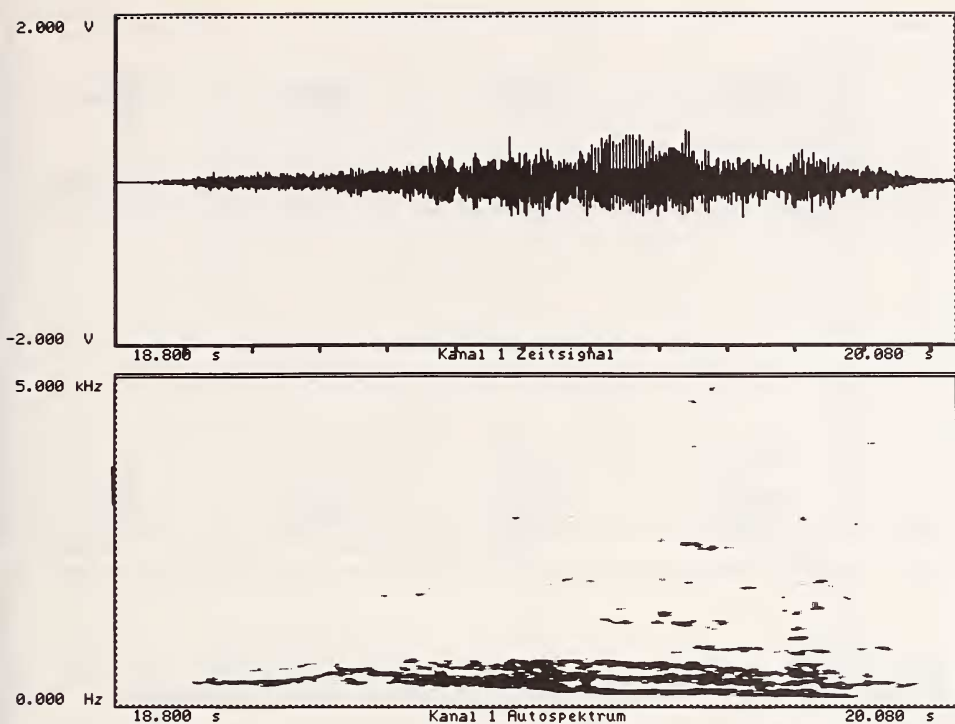


Fig. 6. Oscillogram (top) and sonagram (bottom) of call no. 5 of the roaring sequence shown in Figs. 4 and 5. X-axis (time) is the same for both graphs (1.28 s duration), its subdivisions in the oscillogram representing 0.1 s each. Units and their respective calibrations on the y-axes are given. This call is a main call with grunt element (cf. PETERS 1978)

cat that appears to indicate contentment or pleasure and is believed to result from the streaming of air over the false vocal cords" gives no criteria for an unequivocal structural identification of this felid vocalization, although even making a statement on the supposed mechanism of sound production. In principle, there ought to be less difficulty in correctly identifying purring, because it is such a familiar sound in the domestic cat. Moreover, some of its unique structural characteristics are already identifiable by careful observation without proper bioacoustic analysis. The articulation and structure of purring are so singular that only a vocalization with all its pertinent characteristics (see FRAZER SISSOM et al. 1991), established by bioacoustic analysis (cf. Fig. 8), ought to be so classified.

Anecdotaly, this vocalization has been reported in many felid species, even for most of those that allegedly cannot purr, like lion or tiger, and other *Panthera* species (e.g. HEMMER 1966, 1968; SCHALLER 1972; NEFF 1982). Several authors (e.g. HEMMER 1966, 1968; SCHALLER 1972) maintained that in some of these species purring is articulated during exhalation only. LEYHAUSEN (pers. comm.) holds that very young cubs of the *Panthera* species very likely are able to purr during in- and exhalation. It is highly probable that different types of sounds were lumped under the term 'purring' in various species. Verifiable evidence based on proper bioacoustical analyses for the existence of this vocalization was only presented for relatively few felid species: juveniles of margay (*Felis wiedii*), little spotted cat (*F. tigrina*) and bobcat (*Lynx rufus*), juveniles and adults of the domestic cat, jaguarundi (*Felis yagouaroundi*), puma and serval (*F. serval*), and adults of the Eurasian lynx (*Lynx lynx*), cheetah, and the Indian desert cat (*Felis silvestris ornata*)

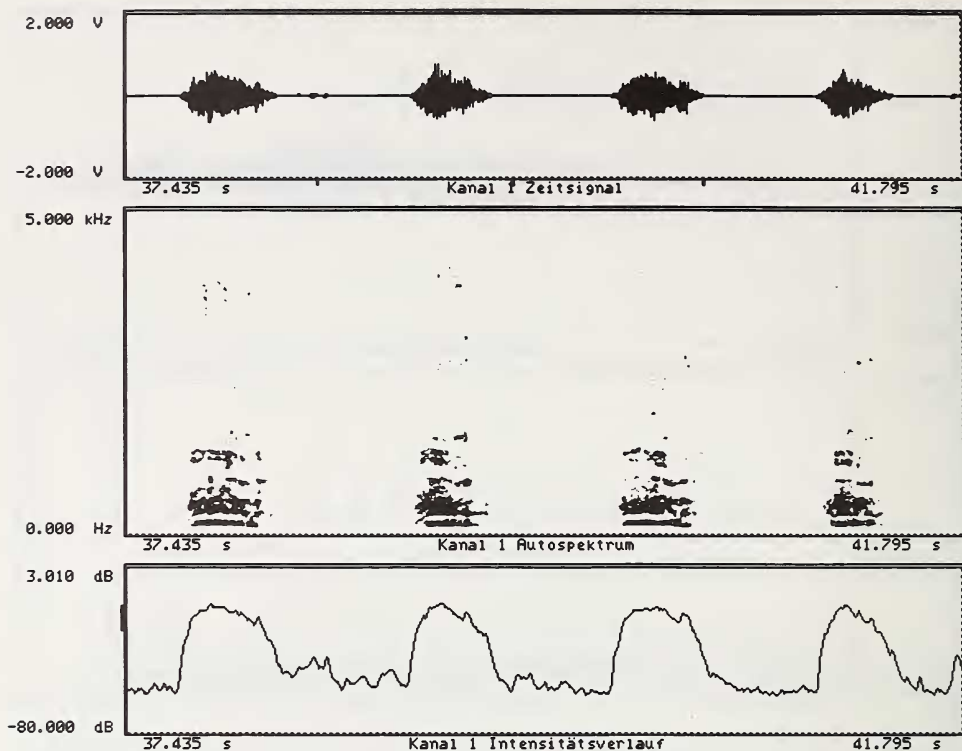


Fig. 7. Oscillogram (top) and sonagram (bottom) of calls no. 17 to 20 of the roaring sequence shown in Figs. 4 and 5. X-axis (time) is the same for both graphs (4.36 s duration), its subdivisions in the oscillogram representing 1 s each. Units and their respective calibrations on the y-axes are given. These calls are grunts (cf. PETERS 1978)

(PETERS 1981). All of these species have a fully ossified hyoid; unequivocal observations and tape recordings of purring in one further species of the Felidae with this type of hyoid morphology exist (see Tab. 2). However, a general statement on a direct correlation between the presence of a fully ossified hyoid in a felid species and its ability to purr can only be made with reservations, since unequivocal evidence of this sound is lacking in too many species of the Felidae which have this hyoid morphology. On the basis of available data, the existence of such a correlation also cannot be refuted, though. In detailed analyses of domestic cat purring (REMMERS and GAUTIER 1972; FRAZER SISSOM et al. 1991), no mention was made of a role of the hyoid in articulating this sound. None of the five felid species with an incompletely ossified hyoid has been examined carefully enough to make a scientifically substantiated statement as to whether they can or cannot purr.

So far, no other vocalizations have been technically described in the Felidae, the distribution of which among the various species of the family matches that of the two hyoid structure types.

As detailed before, the postulated direct correlation of an incompletely ossified hyoid in a felid species and its ability to roar has been refuted. In respect of purring, a definitive statement cannot be made yet as to whether all species with a completely ossified hyoid can purr and whether this vocalization is restricted to these felids. Therefore, the hypothetical correlation of purring and hyoid structure in the Felidae can neither be falsified nor verified at the present state of analysis. Consequently, as this hypothesis is an attempt at explaining

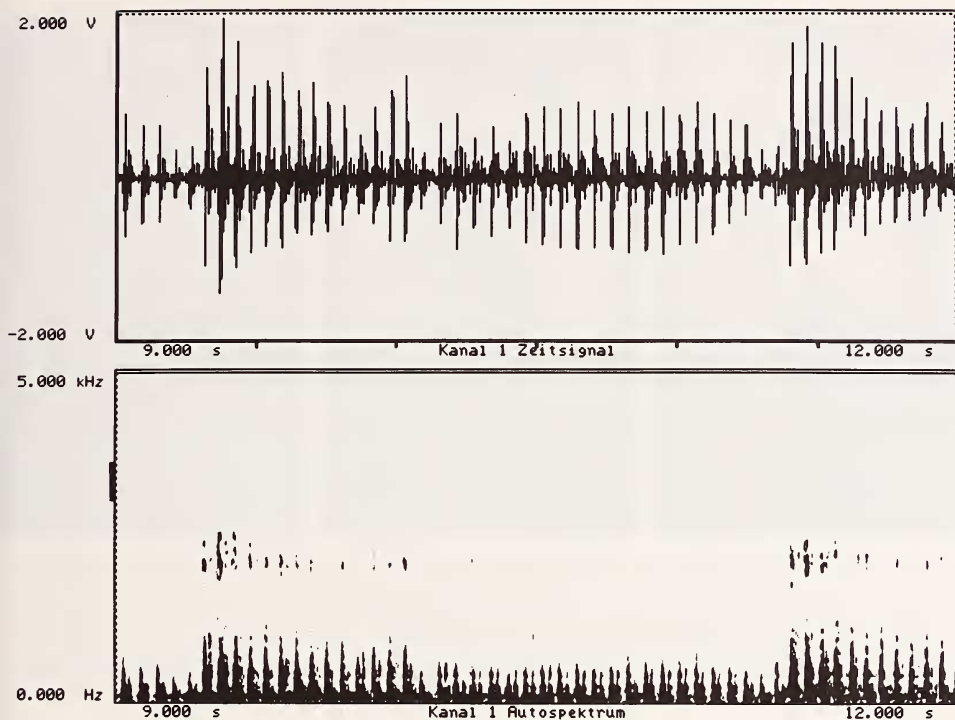


Fig. 8. Oscillogram (top) and sonagram (bottom) of purring of an adult ♀ puma (*Felis concolor*). X-axis (time) is the same for both graphs (3 s duration), its subdivisions in the oscillogram representing 0.5 s each. Units and their respective calibrations on the y-axes are given

the cause of major differences in the composition of acoustic signal systems in felids, it seems to be scientifically more appropriate, for the present, not to maintain it.

Laryngeal anatomy and vocalization

Detailed comparative anatomical studies of the larynx as the sound producing organ had been lacking in the Felidae until very recently (HAST 1986, 1989). Earlier studies of felid larynges by NEGUS (1949), KELEMEN (1963) or SCHNEIDER (1964) did not deal with the interdependence of larynx structure and the acoustic repertoire of a species in a specific way. They only arrived at statements like "The roar of the lion is produced with a comparatively simple vocal apparatus." (KELEMEN 1963: 503) or "The larynx of the felids in general is more primitively constructed than the larynx of the hare or of the antelope, but in spite of this the vocal production of the latter is very much poorer." (KELEMEN 1963: 514). This lack of information exists despite the fact that the hypothetical correlation of hyoid structure and vocalization in the Felidae already was a relatively common view.

The major findings of HAST (1989: 118, 119) are that, of the 14 felid species studied, the larynges of lion, leopard, jaguar, and tiger are exceptional in having a "large pad of fibro-elastic tissue which constitutes the rostral portion of each of the proportionately very large undivided vocal folds". The other species studied are not atypical for carnivores in that they have a "larynx with divided thyroarytenoid folds, with a depression between the rostral and the caudal folds that varies from a slight fossa to a deep ventricle, and a vocal fold with a sharp edge" (see Fig. 9 a-c). The specific structure of thick vocal folds in the

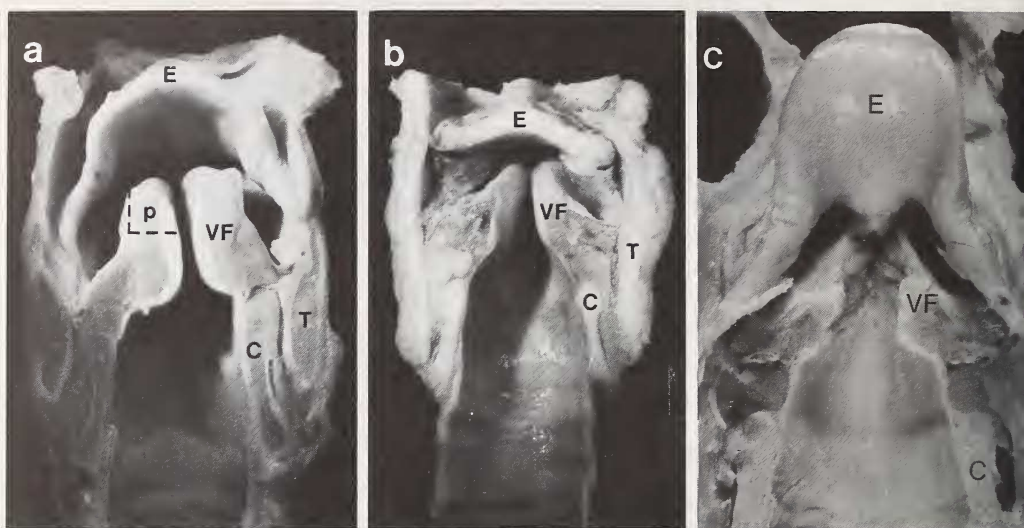


Fig. 9. Dorsal view of larynges of a: a jaguar (*Panthera onca*), b: a snow leopard (*P. uncia*), and c: a puma (*Felis concolor*) cut coronally. The longitudinally very large vocal folds (VF) of the jaguar with their large pad of fibro-elastic tissue (p) are readily distinguished from the proportionately shorter vocal folds of the snow leopard and the even shorter vocal folds of the puma with their sharp edge (E = epiglottis; C = cricoid cartilage; T = thyroid cartilage). (Figures a and b from HAST [1989] with kind permission of the Journal of Anatomy; c: reproduced at a larger scale than a and b)

four species mentioned has the consequence that they are able to produce sounds of high acoustical energy and with lower frequency components than those species with thinner vocal folds (HAST 1989). Additional felid species (*Felis colocolo*, *F. nigripes*, *F. serval*, *F. tigrina*, *F. yagouaroundi*) studied subsequent to HAST (1986, 1989) confirm that only the four species mentioned above have this special morphology of the vocal folds.

The incompletely ossified hyoid also enables lion, leopard, jaguar, tiger, and snow leopard to move their larynx away from the oral cavity, and thus also from the mouth, thereby extending the length of the tube (see Fig. 10 B), which results in an even lowered pitch of vocalization. Consequently, the specific structure of their hyoid can amplify the effect of the thick vocal folds in the former four species quantitatively. However, it is not possible at present to quantify the effect of their unusually shaped vocal folds in deepening and intensifying the calls of these four species.

Generally, species of the Felidae vary considerably in the pitch of their equivalent calls, and no uniform, direct size-correlation is manifest in an interspecific comparison. On the contrary, some felid species with sharp-edged vocal folds (and a completely ossified hyoid) have strikingly high- and low-pitched calls in relation to their position within the over-all size range of the Felidae (this statement also holds for the snow leopard with an incompletely ossified hyoid). In relation to its size, this species' main call is remarkably high-pitched (PETERS 1978). This finding is a caveat that vocal fold morphology (and hyoid structure) alone are not decisive parameters for the pitch of a felid species' calls.

With the exception of a few measurements for lions (JAROFKE 1982), no quantitative data on loudness of felid vocalizations are available; therefore no interspecific comparisons in this respect can be made. Generally, none of the morphological and physiological parameters determining the pitch and intensity of a felid species' vocalizations have been quantified.

HAST (1986, 1989) observed that the specific structure of the vocal folds in the lion,

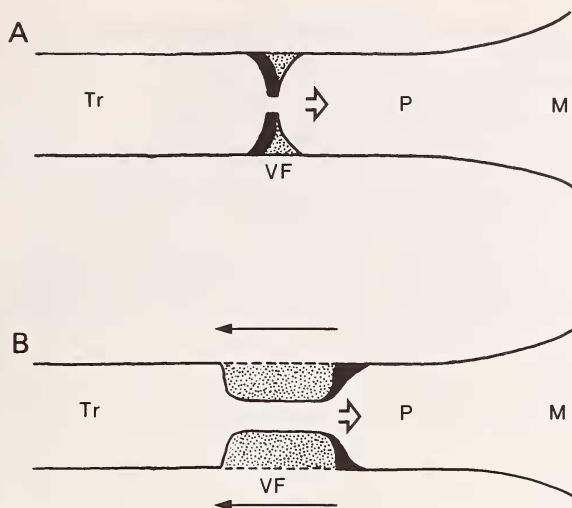


Fig. 10. Schematic drawing of the vocal tract of A: a felid species with sharp-edged vocal folds and B: a felid species with vocal folds with a large pad of fibro-elastic tissue. The open arrows in A and B show the direction of the expiratory air flow. The arrows in B indicate that a hyoid with an elastic ligament instead of a bony epihyoid, which the species with this type of vocal fold morphology have, allows for an elongation of the supraglottal vocal tract, i.e. the distance of the sound generator from the mouth, which results in lower pitch of calls (M = mouth; P = pharynx; Tr = trachea; VF = vocal folds)

tiger, leopard, and jaguar has a qualitative influence on their vocal repertoires, enabling them to roar (although not technically defined). Therefore, according to the above discussions it is not clear to which vocalization(s) this term actually refers in these four species. As detailed before, no matter how roaring was defined by any of the earlier authors, it is not exclusively common to these four species among the Felidae. If the hypothesis of a correlation between vocal fold morphology and vocalization in the Felidae is maintained, to the effect that these morphological characteristics have a qualitative influence on the composition of the vocal repertoire of species, the distribution of vocalization types must be examined. This distribution must be compared to that of the different types of vocal folds in the various species of this carnivore family, especially lion, leopard, jaguar, and tiger, in contrast to the rest of the family. There is but one type of vocalization, the main call with grunt element (Fig. 6), which is common to these four species but not present in any other felid species (PETERS 1978). This call type is a constitutive element in the structured call sequences of the lion (= roaring 'proper') (Figs. 4, 5) and may be present in the equivalently structured call sequences of leopards and jaguars. Tigers utter such calls as single calls or in call series which are irregular with respect to the call types that compose them, the calls' intensity and their temporal sequence (PETERS 1978). Parallel with this character complex, the larynges of these four species have morphological characteristics in common, which distinguish them from those of all other felid species, specifically a large pad of fibro-elastic tissue which constitutes the rostral portion of proportionately very large vocal folds (HAST 1989). However, this concordance/association of characters is not unequivocal evidence that the occurrence of this specific type of vocalization in only these felid species is caused by their special laryngeal morphology. At the present state of analysis no other type of vocalization is known which is shared only by the four species with specific vocal fold type, as opposed to the equivalent character situation in the rest of the species of the family Felidae. Therefore, a qualitative

Table 2. Association of characters of hyoid structure, anatomy of vocal folds and vocalization in species of the Felidae

Species	Hyoid structure	Vocal fold type	Roar	Vocalizations Purr	MC
<i>Acinonyx jubatus</i>	os	s	—	+	—
<i>Felis concolor</i>	os	s	—	+	—
<i>F. geoffroyi</i>	os	s	—	+	—
<i>F. serval</i>	os	s	—	+	—
<i>F. silvestris</i>	os	s	—	+	—
<i>F. tigrina</i>	os	s	—	+	—
<i>F. wiedii</i>	os	?	—	+	—
<i>F. yagouaroundi</i>	os	s	—	+	—
<i>Lynx lynx</i>	os	?	—	+	—
<i>L. rufus</i>	os	s	—	+	—
<i>Neofelis nebulosa</i>	os	s	—	?	?
<i>Panthera uncia</i>	e	s	—	—	—
<i>P. tigris</i>	e	p	—	—	+
<i>P. leo</i>	e	p	+	—	+
<i>P. onca</i>	e	p	+	—	+
<i>P. pardus</i>	e	p	+	—	+

MC: main call with grunt element; os: hyoid completely ossified; e: hyoid with elastic ligament; s: sharp edged vocal folds; p: vocal folds with thick pad of fibro-elastic tissue; character +: present; —: absent; ?: no data/character state doubtful.

influence of vocal fold morphology on a species' vocalization repertoire remains conjectural in the Felidae.

Hyoid structure, laryngeal morphology, and vocalization as characters in felid systematics

Since initial studies by POCOCK (1917b), hyoid structure (and its correlation with vocalization) has remained a major criterion in felid classification above the species level (e.g. CORBET 1978; NEFF 1982). After discussing statements by various authors that lions, tigers, leopards, jaguars and snow leopards (the felid species with an incompletely ossified hyoid which allegedly ought to be unable to purr) can purr, NEFF (1982: 21) concluded "... there is still some doubt about the distribution of the ability to purr among the wild cats." Although she cited data that would refute the postulated correlation of hyoid structure and the presence of roaring or purring in a felid species, NEFF (1982) retained POCOCK's criterion of hyoid structure to separate the subfamilies. Thus, she either regarded the differences in hyoid structure as sufficient to separate the subfamilies of the Felidae, irrespective of whether there is a correlation with vocalization or not — as verified above there is not —, or she doubted reports of purring in species which allegedly are not able to produce this sound because of their hyoid structure. Even very recent classifications of the Felidae based on character complexes like immunological distance or DNA-hybridization data (WAYNE et al. 1989) refer to the differences in hyoid structure as supporting evidence. HALTENORTH (1937), however, expressly denied any systematic significance of hyoid morphology within the Felidae.

If the incomplete ossification of the hyoid is considered as a derived character within the Felidae (cf. SALLES 1992), the monophyletic group characterized by this synapomorphy would include lion, leopard, jaguar, tiger, and snow leopard, irrespective of the rank attributed to this taxon and other characters allegedly/perhaps correlated with hyoid structure. According to various authors, additional synapomorphic characters shared by these five species are: 1. coat pattern on the head completely dissolved into spots (HEMMER

1981) (other authors like LEYHAUSEN [1950] hold another view in respect of this character); 2. bridge of the nose covered with hair up to its anterior edge (HEMMER 1981); 3. simple structure of the baculum without bifurcation in its basal portion (KRATOCHVÍL 1976).

In addition to the above mentioned five species HEMMER (1978) included marbled cat and clouded leopard in the 'pantherine line', based on morphological (see POCOCK 1917a, 1932), ethological, physiological, and karyological data. However, in a later publication on the same topic (HEMMER 1981), the 'pantherine line' did not include the marbled cat. Based on coat colour and pattern, WEIGEL (1961) grouped *Panthera*, *Uncia*, and *Neofelis* in the Pantherinae. In addition to the five species united in this subfamily by POCOCK (1917b), STAINS (1984) included the clouded leopard without giving criteria for doing so; WOZENCRAFT (1989) included lion, leopard, jaguar, tiger, snow leopard, clouded leopard, the marbled cat, the lynxes and the caracal in the subfamily Pantherinae. Based on their comparative biochemical studies COLLIER and O'BRIEN (1985), O'BRIEN et al. (1987) and WAYNE et al. (1989) established a '*Panthera* lineage' with the five roaring (sic) cat species (lion, leopard, jaguar, tiger, snow leopard), the lynxes, and the marbled cat, all of which also share an identical karyotype different from the remaining felid genera (cf. WURSTER-HILL and CENTERWALL 1982). In addition, the '*Panthera* lineage' of COLLIER and O'BRIEN (1985) includes – among others – such diverse species as the African golden cat (*F. aurata*), serval, cheetah, and yagouaroundi (*F. yagouaroundi*).

However, illustrating again the conceptual confusion with regard to 'roaring', WAYNE et al. (1989: 473) listed further characters supporting their classification of the Felidae in stating that "The most recent radiation led to the five species of roaring cats, genus *Panthera*, . . .", and then continue (473, 474) "The lion, tiger, leopard, and jaguar have an incompletely ossified hyoid that allows them to roar and thus unites the group. . . the snow leopard (*P. uncia*), the only nonroaring member of the genus, . . . has a hyoid with structural similarities to the pantherids." (sic).

HAST (1986, 1989) considered the systematic significance of the distribution of the two basic types of vocal fold morphology within the Felidae, especially as regards the content of the genus *Panthera* and the generic association of the snow leopard. Shared acoustical and morphological characteristics in lion, leopard, jaguar, and tiger (presence of main call with grunt element, hyoid structure, vocal fold morphology), may support their joint classification in the genus *Panthera*. The snow leopard shares only one of these three characteristics with the latter four species, the incompletely ossified hyoid. These findings may be taken to support the view of various authors (e.g. POCOCK 1917b; Haltenorth 1937; HEMMER 1966, 1968, 1972, 1981; PETERS 1978, 1980; NEFF 1982) that the snow leopard should be classified in its own genus *Uncia* and not in *Panthera* (HONACKI et al. 1982; CORBET and HILL 1991).

The continuing dispute on the systematics of the Felidae (cf. e.g. SIMPSON 1945; EWER 1973; HEMMER 1978; LEYHAUSEN 1979, 1992; KRÁL and ZIMA 1980; HONACKI et al. 1982; KRATOCHVÍL 1982; COLLIER and O'BRIEN 1985; WAYNE et al. 1989; WOZENCRAFT 1989; CORBET and HILL 1991; KITCHENER 1991; NOWAK 1991; SALLES 1992) is clear evidence that conclusions drawn concerning this matter vary according to character complex(es) studied and their weighting, in view of differences and conformities of character/character state distributions found in species for various complexes.

Together with other morphological character complexes studied, data on hyoid structure, vocal fold morphology and especially vocalization support the hypothesis that *Panthera*, *Uncia* and *Neofelis* form a monophyletic group (cf. HEMMER 1981; SALLES 1992). These characters conflict with chromosomal (KRÁL and ZIMA 1980) and immunological distance data (COLLIER and O'BRIEN 1985), which would ally the lynxes and the marbled cat to this group.

Systematic studies based on any set of genetically determined characters should be congruent with other such studies based on different sets of characters in the same

organisms (HILLIS 1987). The conflict in the Felidae is very likely due to unrecognized character convergencies, mistakes in the interpretation of shared characters/character states as symplesiomorphic or synapomorphic, and the fact that the different character complexes undergo different rates of evolution, with character evolution not generally reflecting group phylogeny. We have not yet arrived at a stage of analysis of the evolutionary history of the Felidae in which congruence/consensus or complementarity of the various character data sets are possible.

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Zusammenfassung

Hyoidbau, Kehlkopfmorphologie und Lautgebung bei Feliden (Mammalia: Carnivora: Felidae)

Bei den meisten Arten der Feliden ist das Hyoid (Zungenbein) vollständig verknöchert, bei fünf Arten der Familie jedoch nicht, sondern enthält ein elastisches Ligament. Dieser Unterschied im Hyoidbau wurde von vielen Autoren als Ursache für die Ausbildung bzw. das Fehlen der beiden Lautformen Brüllen und Schnurren im Lautrepertoire der einzelnen Arten der Felidae angesehen. Hyoidbau und damit hypothetisch korrelierte Lautgebung wurden in der Systematik der Felidae als wesentlicher Merkmalskomplex bewertet. Die vorliegende Untersuchung diskutiert die postulierten Zusammenhänge zwischen Hyoidbau und Lautgebung auf der Grundlage eindeutig definierter Lauttypen und bezieht dabei neue Ergebnisse zur Kehlkopfmorphologie der Feliden mit ein.

Es ist erwiesen, daß nicht alle fünf Felidenarten mit einem unvollständig verknöcherten Zungenbein brüllen können, ein solcher Hyoidbau bedingt also nicht automatisch die Ausbildung des Brüllens. Andererseits findet sich diese Lautform aber auch bei keiner Art mit einem vollständig verknöcherten Hyoid. Alle Arten, bei denen bisher die Fähigkeit zu schnurren gesichert ist, haben ein vollständig verknöchertes Hyoid, für viele Arten mit diesem Hyoidtyp fehlt allerdings bisher noch der eindeutige Nachweis dieser Lautform, so daß eine definitive Aussage darüber, ob ein solcher Hyoidbau für die Ausbildung des Schnurrens notwendig ist und diese bedingt, bisher nicht möglich ist. Das Vorkommen eines weiteren Lauttyps ist auf die vier Felidenarten beschränkt, deren Stimmlippen eine von allen übrigen Arten der Familie abweichende Form aufweisen. Die Aussagefähigkeit dieser Merkmalskomplexe für eine Rekonstruktion der stammesgeschichtlichen Beziehungen innerhalb der rezenten katzenartigen Raubtiere wird erörtert.

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